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REVIEW

Physiology of Penile Erection—A Brief History of the Scientific Understanding up till the Eighties of the 20th Century

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ABSTRACT

Introduction. Understanding the physiology of penile erection is important for all who work in the field of sexual medicine.

Aim. The aim of this study was to highlight and analyze historical aspects of the scientific understanding of penile erection.

Methods. (i) Review of the chapters on the physiology of erection out of the author's collection of books dealing with male sexual functioning published in the German, French, Dutch, and English language in between 1780 and 1940. (ii) Review of the topic "physiology of penile erection" of relevant chapters of *Classical writings on erectile dysfunction. An annotated collection of original texts from three millennia*, including the study of all relevant references mentioned in these books.

Main Outcome Measure. The main outcome measure used for the study was the scientific understanding of the physiology of penile erection.

Results. In Antiquity, Galen considered penile erection as the result the accumulation of air. His ideas so dominated medieval medicine that nearly everyone then alive was a Galenist. The beginning of the Renaissance shows meaningful examples of experimental scientific work on the penis. Da Vinci correctly concluded that erections were caused by blood, and in the 18th century, Von Haller from Switzerland was the first who explained that erections were under the control of the nervous system. In the 19th century, a mindset that emphasized on experimentation determined a new direction, namely experimental physiology. Animal studies clarified that stimulation of the nervi erigentes-induced small muscle relaxation in the corpora cavernosa. Nearly all were published in the German language. That may be one of the reasons that the existence of the concept of smooth muscle relaxation remained controversial until the first World Congress on Impotence in 1984 in Paris.

Conclusions. As the Renaissance's innovative research defined neural and vascular physiologic phenomena responsible for penile erection. The concepts from animal experimentations in Europe in the 19th century significantly contributed to the current understanding of penile erection. **van Driel MF. Physiology of penile erection—a brief history of the scientific understanding up till the eighties of the 20th century. Sex Med 2015;3:349–357.**

Key Words. History; Physiology; Penile Erection

Introduction

Human physiology investigates the mechanisms that keep our bodies alive and functioning. The principal level of focus is at the level of organs and systems within systems. Understanding physiology is one of the basic prerequisites for practicing physicians. In this respect, the mechanisms of penile erection are important for all who work in the field of sexual medicine.

Today, we know that penile erection is a complex physiologic process that occurs through a cascade of neurologic, vascular, and humoral events. This cascade is initiated by auditory, visual, and olfactory signals and local stimuli of the penis. Erection begins with an increased flow in the pudendal arteries and dilatation of the cavernous arteries and helicine arterioles in association with relaxation of the smooth muscles of the trabecular network causing engorgement of blood in the corpora. This leads to compression of subtunical venules by the resistant tunica albuginea. This knowledge is common sense in the 21st century, but one should realize that current understanding of penile physiology has gone through a long evolutionary process. The goal of this article was to summarize and to analyze how the knowledge on the physiology of the penis developed throughout the ages, from Antiquity when the Greeks taught that erection was inflation of air up to the eighties of the 20th century.

Antiquity and the Middle Ages

The study of human physiology as a medical field dates back to the time of Hippocrates (c. 460-c. 370 BC). His intellectual legacy pervaded Western medical thinking until the Renaissance. He stated that erections were generated *pneuma* and *vital spirits* flowing into the penis. In this respect, a proper balance between the four humors, blood, phlegm, yellow bile, and black bile, and the four elements, earth, air, fire, and water, was very important. Hippocrates thought that the testes were connected to the penis by fine cords, like a system of pulleys that could facilitate erection. Damage to these cords, for example by castration, would profoundly affect erectile capability [1]. As in his opinion, semen was the most potent fraction of male bodily fluids Hippocrates also believed that excessive ejaculations could reduce erectile functioning.

Ancient Greek philosopher Aristotle (384–322 BC) stated that penile erection was an "involuntary movement," which could be caused by imagination [2]. As Hippocrates, he outlined the physiologic concept of the necessity of *pneuma* and he theorized that weight behind the testicles could raise the penis, so they acted as a sort of fulcrum. Charis Asvestis briefly summarized Aristotle's thoughts on the physiology in one of the chapters out of *Classical writings on erectile dysfunction* [3]:

> The erection of the human penis occurs through three mechanisms: 1. Imagination, 2 moisture, which increases in the genitals whose passages are full of *pneuma*, and 3. The testicles, which act as a fulcrum.

Without any doubt Galen of Pergamon (129–200/216) was the most famous of the ancient physicians after Hippocrates. Galen's job at a gladiator school early in his career gave him ample access to body wounds in humans, but his medical treatises were for the most part based on classic metaphysics and the dissection of animals [4].

In Galen's view, the primary cause for erection was a specific quality of the corpora cavernosa (CC). He called them "the hollow nerves." They were able to attract the expanding *pneuma* with the aid of connected parts consisting out of arteries, veins, and nerves, and in addition the "internal heat" pushed the penis out from a man's body [5]. Many short case reports can be found in the work of Galen. Thirty-three are dealing with urologic organs or symptoms, seven specifically with the physiology of priapism. In his treatise *On the Affected Parts* Galen gave a sober description: "an increase in the length and circumference of the male genitalia without sexual desire and without the acquired increase in heath which some people experience in the recumbent position" [6]. In his view, priapism was the consequence of a nonnatural condition of the arteries presenting pathologic widening of arterial orifices or in the formation of gaseous *pneuma* in the nerves. According to Foucault, Galen was most often inclined to blame the dilation of arteries: "This kind of disease was found in those who had too much sperm and who contrary to their usual habits abstained from sexual intercourse (unless they found a means of dissipating in numerous occupations the surplus quantities of their blood), or in those who, while practicing self-control, imaged sexual pleasures after seeing certain spectacles or, as a result of recurring memories" [6].

With respect of Arabian medicine, the famous Avicenna (980–1037) was like Aristotle more a philosopher than a physician. While Arab physicians were not allowed to dissect human bodies, their ideas were over all nothing more than summaries of Galen's work. Obviously, examinations of passages dealing with the physiology of erection in his book entitled *De Anatomia Testicularum et Vasorum Spermatis* confirmed the Greek ideas that erection occurred by filling with *pneuma* [7,8].

The 15th–18th Century

One of the first people to study the penis thoroughly was Leonardo da Vinci (1452–1519)

[9–12]. This brilliant man opposed the notion that an erection came about as a result of the accumulation of air. His argumentation was based on physical aspects:

> That would be a vast amount of air, that which enlarges and elongates the penis and makes it as dense as wood, so that the whole great quantity of air in the nerves would not be sufficient for reduction to such a density; not only the air of the nerves, but if the body were filled with it, it would not suffice [9].

Da Vinci only believed what he saw with his own eyes. In 1477 he attended a public hanging, and at the subsequent dissection of this body by anatomists, a practice allowed twice a year by Florentine authorities on dead criminals, he saw what really filled the penis:

> I have seen . . . dead men who have the member erected, for many die thus, especially those hanged. Of these [penises] I have seen the anatomy, all of them having great density and hardness, and being quite filled by a large quantity of blood. . . . If an adversary says wind caused this enlargement and hardness, as in a ball with which one plays, I say such wind gives neither weight nor density. . . . Besides, one sees that an erect penis has a red glans, which is the sign of the inflow of blood; and when it is not erect, this glans has a whitish surface" [9].

In 1573, Ambroise Paré (1510–1590), personal physician of four consecutive French kings and often called the "father of modern surgery," came to the same conclusion in one of his treatises [13]. What Paré did not know was that Da Vinci, a medical amateur, had already written it a century earlier. Sometime around 1503, Da Vinci was quietly given access to unclaimed corpses at a Florentine hospital. He had asked for it because he was convinced that the only way to really know the whole human body was to take it apart and examine the pieces. He did a full study of the body of an old man, the "centenarian" and of a child of 2 years at about the same time [10]. It seems likely that he also dissected a second elderly male, a younger male, and a human fetus of about seven months post-conception, but other dissections were of parts of human bodies.

Da Vinci came close to his goals, but even brilliant men make errors. The anatomic knowledge demonstrated in his observations is full of imperfections. His drawings span the years between 1487 and 1513, but only in the second half of this 25-year period did he gain detailed knowledge through dissections. Initially, he had to gather his information out of books. Direct translations of the original Greek texts into Latin or other European languages became however yet available from 1525 on, 6 years after Da Vinci's death. In addition, Da Vinci was not familiar with Latin or Greek. Probably, the most important book for Da Vinci was an Italian edition of Johannes de Ketham's *Fasciculo di Medicina* published in 1493. This book included a complete translation of *Anathomia*, which was already written in 1316 by Mondino di Luzzi, latinized as Mundinus (c. 1270–1326) [10,11]. Mundinus worked in Bologna in Italy and was one of the first medieval anatomists to perform dissections.

Mundinus's publication was typical of 15th-century medical books while it was essentially an unchecked reissue of ancient anatomic manuscripts. His information was based on Arabian writings, which had been translated from Arabic into Latin in about 1150. The most famous of these writers was Avicenna who in his turn had derived his information from translations of Galen and pre-Galenic Greek texts into Arabic. In fact, Ketham's version of Mundinus was nothing more than a summary of ancient Greek knowledge filtered through three major translations, from Greek to Arabic, from Arabic to Latin, and from Latin to Italian. So, by reading *Fasciculo di Medicina*, Leonardo gained access to the ideas of Hippocrates, Aristotle, and Galen intermixed with later views of both Avicenna and Mundinus.

His drawing of the male genitals, for example, shows that he was clouded by Aristotle as well as Galen. The penis demonstrates two canals, one for urine and one for seed, the last one being connected to the spinal cord (Figure 1). In ancient Greek writing, seed was derived from *spirit*, which was produced out of blood at the base of the brains and transferred to all parts of the body through the nerves, and Aristotle taught that the testes played no role in procreation other than to provide saliva like humor to lubricate the vagina for intercourse. Leonardo drew a large blood vessel passing from the heart to the testicle in an attempt to include Galen's view that the testes manufactured sperm from the blood, so he tried to mix Galenic and Aristotelian theories [10]. For his later drawings, Da Vinci also used dissections of animals as models, for example oxen. This led him astray: he forgot to draw the prostate while these animals have an atrophied one. On the other hand, Leonardo was the first to illustrate the seminal vesicles and the position of the orifices of the ejaculatory ducts [9,11].

Working in Padua, the Belgian physician Andreas Vesalius (1514–1564) published in 1543

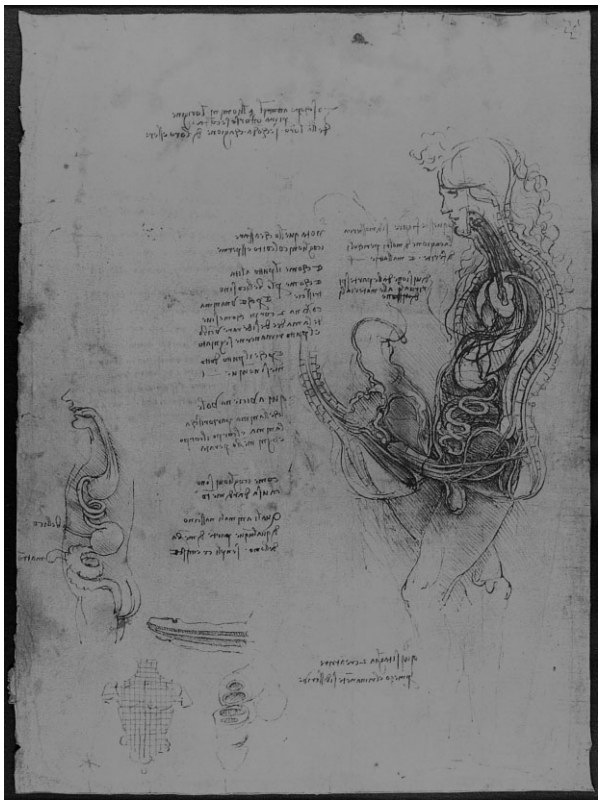

Figure 1 The penis as drawn by Leonardo da Vinci; c.1492–1494. The penis demonstrates two canals, one for urine and one for seed, detail of "The Copulation," "Royal Collection Trust/© Her Majesty Queen Elizabeth II 2015."

his *De Humani Corporis Fabrica Libri Septem* (Seven books on the fabric of the human body) [14]. It became famous for its detailed and beautifully drafted illustrations. Vesalius really broke new ground in the quality of his observations and corrected more than 200 errors made by Galen, but he also duplicated some, for example, the depiction of the vagina as an inverted penis. His description of the function of the penis was rather short: "To this imparted so great a power of delight in the generative act that [men] are incited by this power, and whether or not they are young and foolish or devoid of reason, they fall to task of propagating [as if] they were the wisest of being" [11, p. 67]. According to art historian Patricia Simons, Vesalius visually told the story of the penis as a body part that stood outside because of innately powerful male heat [15] (Figure 2).

She argues that the *Fabrica* shows a penile shaft that mimics erection 'in that it has been stretched out and shown elongated according to Galen's observation. The splayed cleavage of flesh at either side in the area closest to the body in the frontal view is suggestive for forward motion, an impression reinforced by the triangular tip or tapered cone of the glans.' As an art historian, Simons is convinced that this figure was the overture to the penis as a "streamlined, aerodynamic missile like the head of an arrow, spear or dart in which sliced and parted flesh resembles wings or fletched feathers to aid in swift and sure delivery."

Constanzo Varolio (1543–1575) from Italy studied the physiology of erection several decades after Leonardo da Vinci. Because of his early death, his work was posthumously published in Frankfurt in 1591 [16]. According to Sergio Musitelli, some historians have incorrectly written that Varolio assumed that the contraction of the ischio- and bulbocavernous muscles prevented

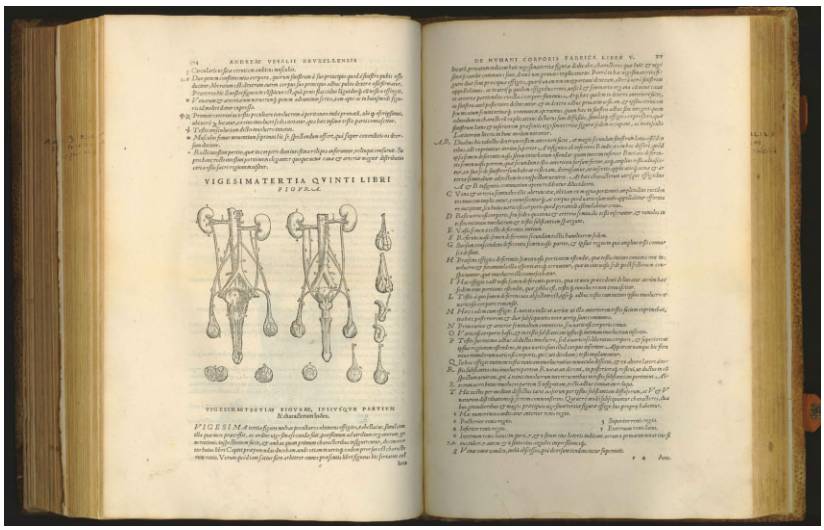

Figure 2 Andreas Vesalius, male organs of generation, *Fabrica*, Basel: Johannes Oporinus, 1555, Book V, figure 23, p. 374. By courtesy of "Erfgoedbibliotheek Hendrik Conscience, Antwerpen," cat.nr. J 5833.

venous reflux [17]. On the basis of his ignorance of the blood circulation, this seems to be nonsense. Varolio adhered to the idea that blood flowed through veins and *spirit* through arteries.

Reinier de Graaf (1641–1673) from the Netherlands, who like Varolio died at a very young age, invented a type of syringe with which he carried out many different kinds of research on dead bodies. When he injected water into the hypogastric artery he saw to his amazement the erectile tissue in the penis filling up, more or less confirming Varolio's conclusions. Way ahead of peers he declared that the key event in erection was not getting blood into the penis, but *keeping it there* [18,19]. In 1668, De Graaf completed his study of the male sex organs. As some researchers today, he was well aware that the male sex organ was a tricky subject, as "disrespectful, lewd people will try to misuse what I publish for wanton images and smutty jokes." His defense was that he had presented his finding in as decent a way as possible, so that "no one can take the slightest offense, unless they are determined to do so" [20]. De Graaf examined the penis as a well-designed tool. He noted the absence of fat under the skin, and how that skin was thinner, looser, and more elastic than just about any other patch of skin of the human body, factors that enabled the penis to become bigger and rigid. Fortunately, his work did not die with him, while another Dutchman, Frederik Ruysch (1638–1731), using the syringes invented by De Graaf in combination with his self-made, secret injecting fluids, became able him to manufacture wax-like casts of the male member [21]. With a never shown thoroughness, these replicas of the penis with all its arteries, veins, and capillaries revealed the expanding and shrinking organ to be a wonder of engineering. In the 18th century, Albrecht von Haller (1708–1777) from Switzerland would become the first who explained erection as an increase of blood flow *under control of the nervous system* [22]. He refused to accept the age-old concept of a fluid traversing the nerves as the cause of nerve-action. He focused his observations on the nerve fiber itself, demonstrating clearly that while "irritability" was a property of muscle fiber, another factor, and 'sensibility was characteristic of nerves.

The 19th Century

At the end of the 19th century, the Austrian physician Victor Vecki von Gyurkovechky (1857–1938) wrote a monograph on what he called *Pathologie und Therapie der Männlichen Impotenz* [23]. Chapter III of the English translation summarizes the scientific knowledge on the physiology of the sexual act including the discourse on penile erection [24]:

> These small hollow interspaces of the three corpora are coated with endothelium resembling that of the veins, and are consequently venous spaces. Numerous emissaries keep all the corpora in communication with one another, and open out into the vena dorsalis and the vena profunda penis. In the base of the penis there are the arteriae helicinae, which are wound in the shape of a ram's horn, in order that they may yield to the changes of volume in the erectile tissue. It is now clearly demonstrated that erection is caused by filling of these spaces with blood, but the entire process of erection is nevertheless far from being explained.

Further, he referred among others to research on this topic by famous European scientists as Albert von Kölliker (1817–1905) from Switzerland, Carl Langer (1819–1887) from Austria, Conrad Eckhard (1822–1905) from Germany, Charles Marie Benjamin Rouget (1824–1904) from France, Friedrich Leopold Goltz (1834–1902) from Germany, and Otto Christian Lovén (1835–1904) from Sweden [25–30]. All of them were entirely men of the laboratory and their scientific work felt within the context of the general transformation that medicine underwent in the 19th century: a mindset that emphasized on experimentation determined a new direction, namely "experimental physiology." Lacking laboratories and communities of scientists essential for much of the work in basic sciences, the United States contributed nothing to penile physiology in those days.

In 1889, Vecki qualified the results of the aforementioned European scientists as being "highly meritorious," but the mechanism of erection still had its mystery. Either the outer transversely striped muscles ventral of the penis or the inner smooth muscles exercised pressure on the efferent veins, so without any doubt the investigators in the 19th century were all well aware of Galen's hypothesis that venous shutdown was important for erection. In 1862, Langer from Vienna theorized that intrinsic contraction of the veins in the plexus of Santorini could induce erection [26]. However, based on his histologic studies, Von Kölliker (Figure 3) had already concluded in 1852 that the CC were capable of active relaxation and contraction [25]. The fact that warmth caused dilatation and cold a contraction of the penis spoke with some force for the influence of the smooth muscles. Von Kölliker concluded that detumes-

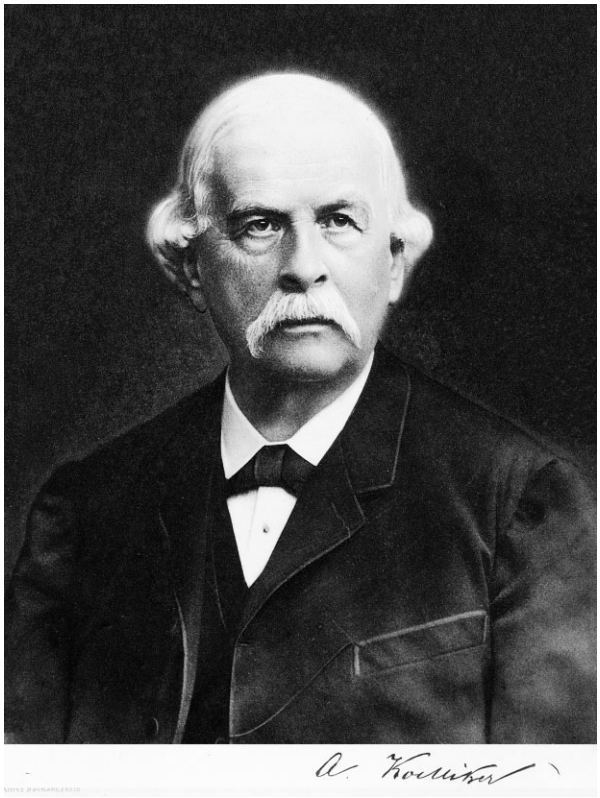

Figure 3 Albert von Kölliker (1817–1905), physiologist and histologist from Würzburg. Source: Wikipedia.org.

cence was likely due to smooth muscle contraction within the corpora. Opposite to his opinion was the theory that the smooth muscles in the spongy tissue did not possess alone sufficient strength and energy to influence erection to such a degree. In his book, Vecki also discussed how the arterial inflow could increase. He suggested that the acceleration of the heart action at sexual excitement could have but a very slight influence (p. 54). However, the main point of discussion was if sexual excitement had a "paralyzing influence on the muscles of the walls of the penis or an invigorating effect causing the contractions to become more frequent, and the arteries to pump, so to speak, a greater quantity of blood into the meshlike spaces of the penis".

With regards the nervous control, Goltz shared the opinion of those physiologists who compared the connection of the nervi erigentes with the penis to that of the nervus vagus to the heart [29]. He stated that the progress of blood flow into the penis was considerably hindered during the time of physiologic rest, while the small penile arteries and other vascular spaces were in a state of moderate contraction. This state was maintained by action of ganglia whose presence had been proven by Lovén [30]. At the end of his review Vecki cites out of Goltz's work and emphases the importance of the cerebrum:

> Experience teaches us that erection can be either caused or checked by different impressions from the most varied parts of the body. It is certain, however, that the cerebrum is the place of origin of the sensations of sexual excitement. With this higher center is connected, by intercentral nerve-channels, an inferior, mechanical reflex center, which has its seat in the lumbar region of the cord, and governs the performance of the act of copulation.

In his classic article out of 1863 about neurophysiologic studies in dogs, Eckhard reported that during the tumescence phase, caused by neural stimulation, the effluence of blood from engorged erectile tissue and the dorsal vein was about 8–15 times greater than in the flaccid state [27]. After a transverse incision of an erect penis, he ascertained that the effluent blood was never only of venous origin and erection consequently was not merely the result of venous congestion, as had previously been thought. He also found that the erected penis contained eight times more blood than in its flaccid state. Lovén supported his results by his finding that when the nervi erigentes were stimulated, the arterioles of the spongy cavernous tissue dilated and arterial inflow markedly enhanced [30]. At the end of all his experiments, Eckhard was really convinced that the vasodilatation caused by the nervi erigentes increased the inflow of blood into the penis and he deduced that the pressure in the wall of the penile arteries during the initial phase of erection had to decrease [31].

At the end of the 19th century more detailed contributions on the physiology of erection were made by John Newport Langley (1852–1925) and Hugh Kerr Anderson (1865–1928) from England [32]. Without any doubt, all the aforementioned concepts derived from animal studies in the century of experimental physiology significantly contributed to the current understanding of erection.

The First Part of the 20th Century: Wrong Tracks

In 1933, William Henry Howell (1860–1945) from Johns Hopkins University had recorded in advance a surprising modern hypothesis about the physiology of penile erection [33]. He wrote that "tumescence occurred while dilatation of small arteries and arterioles caused the CC to distend

with blood under high pressure limited by the tunica albuginea. And full erection required partial occlusion of venous outflow, probably by compression of the afferent veins by the ischio- and bulbocavernous muscles and to a certain extent by the intrinsic musculature of vessel walls." At that time, many other eminent physiologists doubted the role of these muscles or suggested that contractions of the ischiocavernous muscles only had a minor role in producing a full erection [34]. There were other wrong tracks. In 1900, the Austrian anatomist and histologist Anton Gilbert Victor von Ebner (1842–1925) discovered what he called "pads," consisting out of columns of smooth muscle cells within the intima of the arteries to the penis [35]. These intravascular protrusions had already been described by Ercolani in 1869, and in the distant past by anatomists of the famous school of Padua [36]. Von Ebner concluded that those "pads" enabled the arteries by themselves to regulate the blood flow into the penis: "Opening up allowed blood to enter the corpora and closing down later to trap that blood, thereby causing an erection." This theory was widespread wisdom until 1952, when it was updated by the Italian urologist Giuseppe Conti [37,38]. He postulated that erection was caused by three mechanisms: shunting of arterial blood to the corpora, a decreasing blood flow to the penis by contraction of so-called "cushions" in the small arteries and, the trapping of blood in the corpora by similar "cushions" in the efferent veins. Conti concluded that these were the mysterious shutdown valves physiologists had been searching for so long. Blood entered the penis, the corpora expanded, and the "cushions" outside the tunica closed down resulting in an erection. It was as simple as that. However, many years later it was determined that Von Ebner's "pads" and Conti's "cushions" were atherosclerotic debris, much like that found in coronary arteries [39].

In the meanwhile Deysach discussed the validity of animal findings for human physiology [40]. He claimed dissimilar mechanisms in two major groups of animals: "(i) Those with a long os penis as the dog, in whom erection was 'arterial' while it could be induced in the dead animal by perfusing the aorta, and (ii) those without a long os penis as the human where there was a 'venous' erection." In this group he believed blood was trapped in the CC by the active closure of "sluices" between their venous spaces and the deep penile veins. He based this theory on observations made during injection of India ink and vermilion cinnabar into vessels of dogs, deer, elk and monkeys. In retrospect, these "sluices" were very probably the openings of the subtunical venous plexus. More than hundred years earlier John Houston from Ireland even had suggested that in dogs the deep dorsal vein could be restricted by the so-called ischio-urethral muscle [41]. In 1964, Herbert Newman and coworkers still had serious doubts with regards the necessity of venous occlusion for erection [42]. They simply argued that during normal erection, the penis did not become cyanotic whereas experimental restriction of its venous return by an inflated pediatric blood pressure cuff at the base of the penis produced cyanosis and edema without erection. Despite this incorrect reasoning, their study would become the origin of cavernosometry, a technique to study the venous closure mechanism during erection [43].

Conclusions

That an intact neurovascular system and smooth muscle relaxation in the CC are important for erection is common sense in the 21st century, but one should realize that current understanding of its physiology has gone through a long evolutionary process. In Antiquity one thought that vital *spirits* induced erections and that the erected penis was filled with air. Medieval European scientists became corrupted into the idea that air under pressure produced penile rigidity. Thanks to Da Vinci, Varolio and De Graaf and a series of eminent European experimental physiologists in the 18th and 19th century we now know that an erection is produced by a surge of blood under nervous control.

The major breakthrough of the 20th century occurred just as in the 19th with the development of experimental animal models in which erection could be initiated and sustained by stimulation of the cavernous nerves [44]. Virag's and Brindley's experiments in the early 1980s of the 20th century confirmed what physiologists as Albert von Kölliker in the 19th already had hypothesized: the importance of the smooth muscle cells in the CC [25,45,46]. However, the very existence of smooth muscle relaxation and contraction in the CC remained controversial until the first World Congress on Impotence in 1984 in Paris [47].

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Conflict of Interest: Speaker for GSK and Lilly, the Netherlands.

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